Fall 2015

Lingcod (Ophiodon elongatus) Habitat Associations: Implications for Conservation and Management

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LINGCOD (*OPHIODON ELONGATUS*) HABITAT ASSOCIATIONS:

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

A Thesis

Presented to the

Faculty of the

Division of Science and Environmental Policy

California State University Monterey Bay

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Applied Marine and Watershed Science

by

Megan Bassett

Fall 2015

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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ABSTRACT

Lingcod (*Ophiodon elongates*) habitat associations: implications
for conservation and management
by
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Master of Science in Applied Marine and Watershed Science
California State University Monterey Bay, 2015

Understanding the spatial distribution of marine species and the temporal and spatial scales of the processes that drive those distributions continues to be limited, but is increasingly more critical with the implementation of marine spatial planning. Lingcod (*Ophiodon elongatus*) are a common demersal fish found from southern Alaska to Baja California, and are exploited both commercially and recreationally across the entirety of their range. Due to stock declines, Lingcod are managed using a variety of fisheries management tools, including spatial management. This study represents a unique *in situ* investigation of demersal habitat utilization by Lingcod at the southern portion of their range (Point Arena to Morro Bay, California). We used ROV and towed camera sled derived underwater video imagery, coupled with high-resolution bathymetry data, and Generalized Linear Models to investigate: a) how Lingcod are distributed relative to seafloor habitats along California's central coast, b) the extent to which any ontogenetic patterns varied significantly across those habitats, and c) how associations based on visual observations compare to those from landscape modeling analysis. We then extrapolated habitat associations, found in the landscape modeling analysis, beyond the sampled areas to broader areas of the coast by creating habitat suitability maps. The results of this study clearly depicted an ontogenetic shift in Lingcod habitat utilization across the southern end of its range. Lingcod shifted from primarily low relief, soft sediments as young to mixed substrates at intermediate ages and ultimately to primarily harder substrates as adults. However more nuanced associations were also discovered, such as year 2 Lingcod associating with wave relief in soft sediments. These results are important in the context of on-going marine spatial planning wherein further information on the habitat associations of targeted species can allow for more refined management.

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ACKNOWLEDGEMENTS

I would like to start by thanking my advisor, Dr. James Lindholm. His guidance and mentorship over the many years we have worked together is greatly appreciated. I would not be the scientist I am today without him. Dr. Rikk Kvitek – thank you for all of the amazing bathymetry data. I appreciate not only that you and your team collected this amazing resource, but that you make it accessible. Dr. Corey Garza- thank you for always pushing me to think beyond my study; it is truly a better project for it. Deb Wilson-Vandenber- thank you for agreeing to be on my committee; I know you are very busy, but truly enjoyed reading your comments and discussing how my project can be applied to management. I look forward to working with you in the future.

I would like to thank everyone at the Institute for Applied Marine Ecology (IfAME). I had the pleasure of working at the IfAME for over seven years and met some amazing people that have a special spot in my heart.

This project was funded through a collaboration between the IfAME and the Monterey Bay National Marine Sanctuary (MBNMS). I appreciate that I was allowed to work on this project and collaborate with some wonderful people. I gained so much from working with the MBNMS staff and am grateful for their collaboration and teachings. This project was also supported by the California State University Council on Ocean Affairs, Science and Technology and the Undergraduate Research Opportunities Center.

Finally, I would like to thank my friends and family. My time as a CSUMB student is something that I will never forget and I truly cherish the relationships I’ve made along the way. I could not have done this without the love and support from my family. They didn’t know why I chose marine science, being prone to sea sickness, but loved me and supported my choices anyway. My husband Ryan has always supported my passion for the ocean and studying the organisms that reside there. I love you and thank you for everything.

CHAPTER 1

INTRODUCTION

Understanding the spatial distribution of marine species and the temporal and spatial scales of the processes that drive those distributions continues to be limited (Pittman et al. 2007). The subtidal landscape is composed of diverse habitat patches, occurring across multiple different substrate types, and resulting in patchiness of associated organisms, (Greenfield and Johnson 1990; Auster et al. 1995; Anderson and Yoklavich 2007; Anderson et al. 2009; Chang et al. 2010). Landscape ecology is now increasingly being used to investigate and understand the distribution of marine organisms (Turner 1989; Irlandi et al 1995; Bell et al. 1997; Grober-Dunsmore et al. 2008; Hinchey et al. 2008; Pittman et al. 2007). As in terrestrial systems, the level of heterogeneity of a particular landscape is strongly dependent on the scale at which the environment is studied (Turner 1989; Syms 1995). Similarly, the way in which organisms associate with habitat attributes also differs with scale (Syms 1995; Chittaro 2004; Anderson and Yoklavich 2007). At fine scales, fishes may associate with specific features, such as a boulder or depression (Risk 1972; Auster et al. 2003; Auster and Lindholm 2005; Lindholm et al. 2007), while at larger scales the same species may be correlated within a latitudinal (Witman et al. 2004) and/or a depth range (Bergen et al. 2001; MacPherson 2003).

Lingcod (*Ophiodon elongatus*), a common demersal fish along the west coast of North America, exemplifies this diverse association with the landscape. At a fine scale (meters) Lingcod inhabit low relief soft sediment as juveniles and moderate relief rocky reefs as adults (Shaw and Hassler 1989; Petrie and Ryer 2006). At a large scale Lingcod are distributed by depth, located nearshore as pelagic larvae, and to a depth of approximately 400 m as large adults (Miller and Lea 1972; Eschmeyer et al. 1983; King and Withler 2005). The process underlying this ontogenetic shift in habitat associations has not been investigated in detail to determine where these shifts in habitat occur and if they are consistent with our current understanding. Lingcod are known to be cannibalistic, possibly resulting in young individuals settling in soft sediment to avoid adult Lingcod

(Shaw and Hassler 1989). Many studies have been conducted on the movement and home ranges of Lingcod (Martell et al. 2000; Matthews 1992; O'Connell 1993; Yamanaka and Richards 1993), yet these have focused on their northern range (Alaska to Oregon) and have not examined the specific habitats Lingcod use.

Determining Lingcod habitat associations has been improved by advances in geospatial technology, such as geographic information systems (GIS) and benthic seafloor mapping techniques (Hirzel et al. 2002; Rottenberry et al. 2006; Hinchey et al. 2008). Coupling these new landscape modeling technologies with video imagery of the seafloor allows us to explore the patterns of species distributions as well as the ecological and physical processes driving the distributions. We can then extrapolate patterns beyond physical observations to larger geographic areas. The versatility of this technique in marine systems has been highlighted by studies assessing habitat associations of various rockfish species (*Sebastes rosaceus, S. flavidus and S. elongatus)* (Young et al. 2010) and extrapolating those models beyond the initial study area (Iampietro et al. 2008).

Precise knowledge on the distribution and habitat associations of Lingcod are vital to successful management of the species. Lingcod were declared overfished in 1997 from Washington to California (Jagielo and Hastie 2001). Through successful use of more restrictive fishing regulations including large area closures and size restrictions, coupled with favorable oceanographic conditions for recruitment, Lingcod stocks were declared rebuilt in 2005 (Jagielo and Wallace 2005). This population rebound has provided a unique opportunity to study the habitat associations of Lingcod at a healthy population to further inform, and potentially improve, the management strategies for this species.

This study represents a unique in situ investigation of the habitat utilization and ontogenetic movement of Lingcod across approximately 600 linear kilometers of coastline. We employed two assessment methods, using underwater video imagery and high-resolution bathymetry data to investigate the habitat associations of Lingcod at several year class stages. Generalized linear modeling techniques were employed to quantify a) the spatial scales at which Lingcod of different size classes associated with specific seafloor habitat attributes, and b) the extent to which any ontogenetic patterns varied significantly. Models were then used to extrapolate habitat utilization patterns beyond the relatively limited areas actively sampled to broader areas of the coast.

Information on Lingcod in California is limited. Furthermore, a study of this nature, investigating specific habitat associations from visual surveys, has not been conducted on Lingcod outside of one study conducted in Alaska (Starr et al. 2005). Due to the limited amount of information, we sought to answer the questions: 1) How are Lingcod distributed relative to seafloor habitats along California's central coast? 2) Is there a difference in habitat associations of Lingcod at different age classes? and 3) To what extent do associations based on visual observations compare to those from landscape modeling analysis?

CHAPTER 2

METHODS

STUDY AREA

Sampling was conducted along the central coast of California, ranging from Point Arena in the north to Morro Bay in the south (Figure 1). Specific study sites varied in substrate composition from unconsolidated soft sediments (e.g. north Monterey Bay and Morro Bay) to high relief rocky reefs (e.g. Farallon Islands and Point Sur).

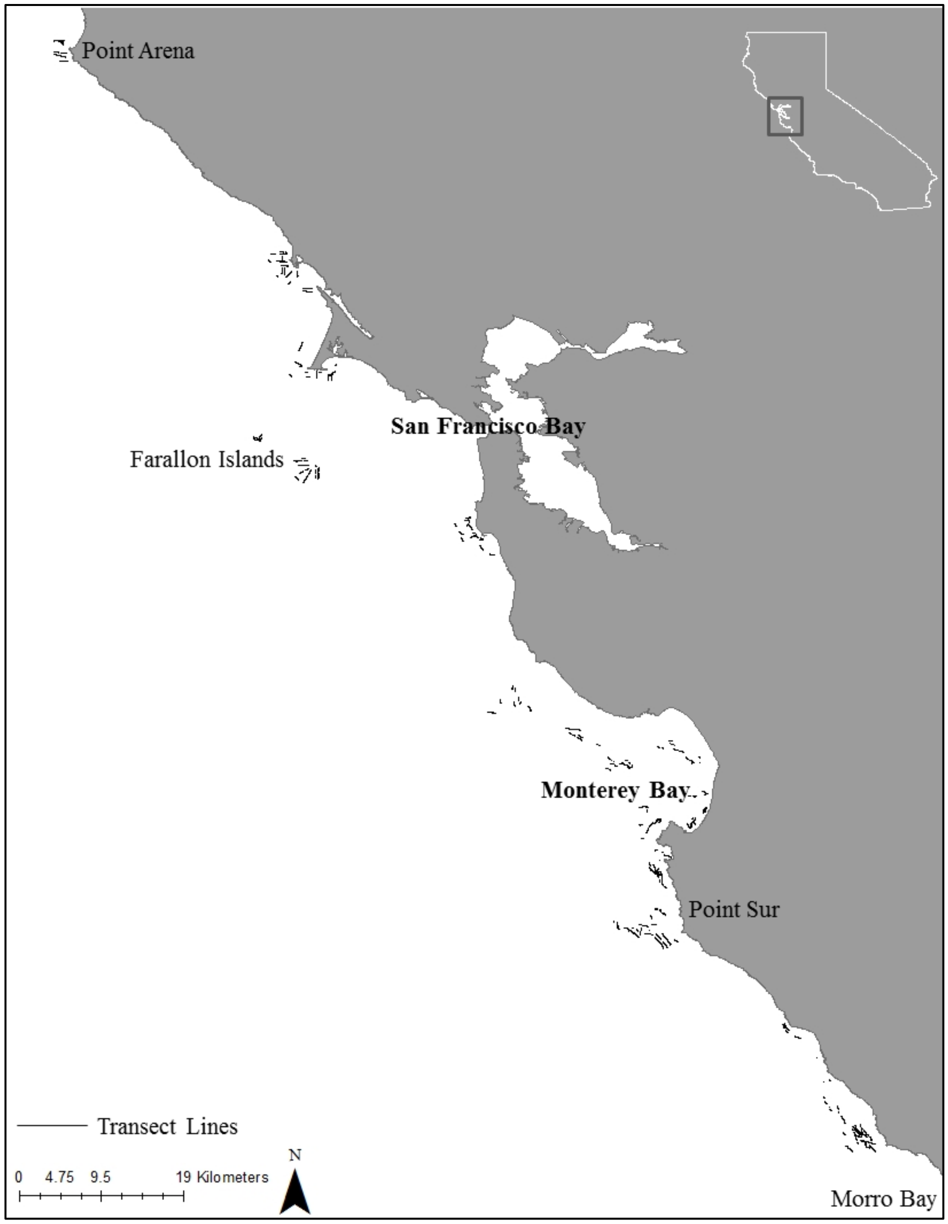

Figure 1 Map of study area from Point Arena in the north to Morro Bay in the south. Dark lines represent individual transects conducted from 2007 to 2013.

FIELD COLLECTION OF VIDEO IMAGERY

Underwater surveys were conducted from 2007 to 2013 (June through October) using both a towed camera sled and a remotely operated vehicle (ROV) at depths ranging from 15 to 500 meters. The sled (Deep Ocean Engineering and Research) consisted of a steel frame (190 × 44 × 52 cm) protecting a single, forward-facing high-resolution color camera with paired 500 mW lasers spaced at 10 cm, two 250 W tungsten/halogen lights, an altimeter, and an electronics cylinder. The cylinder contained circuitry and served as a junction to supply power and to communicate imagery and data (depth, heading, altitude) with the surface system via the 16-pin 250 m armored coaxial cable tether.

The Vector M4 ROV (Deep Ocean Engineering and Research) was equipped with forward-looking standard and HD video, down-looking video and a digital still camera and strobe. Two Quartz halogen and HMI lights, provided illumination for the video. Paired forward- and down-looking lasers provided reference points within the area imaged by each camera. The ROV was also equipped with an altimeter, forward-facing multibeam sonar, and conductivity, temperature, depth (CTD) sensor.

Both vehicles were “flown” at a mean altitude of 0.2 meters above the substrate and at a speed of 0.5 to 0.75 knots. The position of the ROV relative to the vessel was monitored using a Trackpoint III system with an angular accuracy of 0.1 degrees. Vessel position was used as a proxy for the position of the towed sled, which was actually deployed as a drift camera directly below the vessel.

DATA EXTRACTION FROM VIDEO IMAGERY

The associated substrate, relief, water depth, and the total length (TL) were recorded from the video imagery for each individual Lingcod. The geographic coordinates of each individual were later gathered using the unique date-time code in the navigation files.

Substrate was classified according to modified version of Greene et al.’s (1999) habitat classification scheme. Sand and mud substrates were classified as soft sediment (S), while hard substrates were classified as small rock (SR) (gravel to cobble), large rock (LR) (boulders) or continuous rock (CR) (exposed bedrock or reef). Both primary and secondary substrates were characterized for each Lingcod observation. Primary substrate was classified as greater than 50% of the frame and secondary substrate is classified as 20% or greater of the remaining frame (Yoklavich et al. 1999), where a frame was considered the area within view when the video was paused for data collection.

Relief was classified into one of four categories: low (L), wave (W), moderate (M) and high (H). Low relief is classified as one meter or less, wave was classified as distinct peak and trough patterns present in soft sediment, moderate is one to three meters and high is over three meters high off the seafloor. Height off the seafloor was estimated using the ten centimeter sizing lasers on the ROV and camera sled. Similar to the substrate classification, primary and secondary relief were characterized for each Lingcod observation. Fish size was estimated to the nearest 5 cm using the 10 cm paired sizing lasers attached to both the ROV and camera sled. In select cases, the size could not be determined and the fish was recorded, but not included in the size specific analyses.

Latitude and longitude coordinates for each observation were extracted from the Trackpoint III ® acoustic tracking system on the ROV through the Hypack ® navigational software. These coordinates were incorporated into the creation of the habitat suitability maps as they provide precise points where Lingcod were observed. Lingcod location was recorded as ROV position. The camera sled is not equipped with an on-board tracking system. Since there is no reliable way to track the camera sled, it was not incorporated into the GIS habitat suitability modeling.

DATA EXTRACTION FROM DIGITAL ELEVATION MODELS

Bathymetry digital elevation models (DEM) were collected and compiled for the entire study area at a 5 meter resolution (Point Arena to Morro Bay, CA). Several rasters were created from the bathymetry DEM, including: slope, vector ruggedness measure (VRM), topographic position index (TPI) TPI_{20}, TPI_{40}, aspect, and distance from rock. These variables are widely used in this type of habitat modeling because they portray various aspects of the seafloor (Iampietro et al. 2008; Young et al. 2010).

DATA ANALYSIS- FINE-SCALE MODELING FROM VISUAL ANALYSIS

Generalized linear models (GLM) were created in the statistical package R (R Development Core Team 2010) to test which of the predictor variables best described Lingcod distribution. Models were subsequently compared using Akaike's Information Criterion (AIC). Non-detection points were randomly generated from the navigation data. The points were constrained to the transects because they represent true non-detection points of places where we looked and did not find a Lingcod. The number of non-detection points was equal to detection points in order to achieve standardization.

Lingcod were binned by size to determine if a significant difference in habitat associations, or an ontogenetic shift, could be detected (Table 1). Total length was used to determine what habitats specific age classes are associating with (Shaw and Hassler 1989). After three years, male and female growth rates diverge and are varied (Shaw and Hassler 1989). Because of this divergence, Lingcod larger than 50 cm were binned into one category of 3+ years.

Table 1 Lingcod total length (TL) in centimeters and the corresponding age group in years.

TL (cm)	Age (years)
27	1
47	2
50+	3+

Akaike's Information Criterion (AIC) was used to rank each model to determine the extent to which each model, or combination of models, best explains Lingcod habitat associations (Burnham and Anderson 2002).

DATA ANALYSIS- LANDSCAPE MODELING & HABITAT SUITABILITY MAPPING

Habitat suitability maps were created using the Marine Geospatial Ecology Toolbox (MGET). This method has proven useful in mapping areas that are optimal for specific species by extrapolating beyond surveyed areas using known important habitat features (Iampietro et al. 2008; Young et al. 2010). MGET is unique in that it links the geographic information system ArcGIS to the statistical package R (Roberts et al. 2010).

Lingcod detection points were imported into ArcGIS 10.1 using the associated latitude and longitude coordinates collected during video collection. Because the towed camera sled did not have tracking equipment, those Lingcod observations were omitted from this spatial analysis. Non-detection points were then randomly generated along the transect lines using a 5m buffer around the detection points to ensure that detection and non-detection points did not overlap with one another. GLM models were then run and compared using AIC to determine which variables best explain Lingcod distribution.

CHAPTER 3

RESULTS

This study covered approximately 587 km of seafloor from Point Arena to Morro Bay, California. A total of 1476 Lingcod were observed, ranging from 5 cm to 90 cm in TL. The shallowest depth at which a Lingcod was observed was 17 m water depth, while the deepest was observed at 350 m water depth. Of the 1476 total Lingcod observed, 390 individuals were unable to be measured due to poor visibility.

FINE-SCALE MODELING FROM VISUAL ANALYSIS

A total of 83 models were compared for all Lingcod observations to look at general habitat associations. All 1,476 Lingcod observations were used in this analysis, including measured and unmeasured individuals. When models were compared using AIC, the best model was more than two ΔAIC from the next model. This model included the predictor variables: primary relief, secondary relief, combined substrate, and Lingcod size.

Lingcod had a significant negative association with the combination of soft sediment substrate and areas with primary and secondary low relief (Table 2). All Lingcod had a significant positive association with mixed and most hard substrate types, as well as moderate and high relief areas. Size was not significant in this model; however it is present in the top five best performing models. Furthermore, when size was removed from the winning model, its performance dropped from first to 56 out of 83, indicating that, although not significant, size does play some role in the distribution of Lingcod.

Table 2 Significant variables for the best model for Lingcod of all size classes. This model included combined substrate, primary and secondary relief, and Lingcod size. Substrate combinations include: soft (S), small rock (SR), large rock (LR), and continuous rock (CR) substrate types. Relief types include combinations of low (L), wave (W), moderate (M), and high (H).

	Predictor Variables			
Age Class	Substrate		Relief	
All	Soft (Combined)	SS (-) $p < 0.001$	Primary	L (-) $p < 0.001$
	Hard (Combined)	SRSR (+) $p < 0.001$		W (-) $p = 0.258$
		SRLR (+) $p < 0.001$		M (+) $p = 0.008$
		LRSR (+) $p < 0.001$		H (+) $p < 0.001$
		LRLR (+) $p < 0.001$	Secondary	L (-) $p < 0.001$
		LRCR (+) $p < 0.001$		W (+) $p < 0.001$
		CRSR (+) $p < 0.001$		M (+) $p = 0.011$
		CRLR (+) $p = 0.003$		H (+) $p < 0.001$
		CRCR (+) $p = 0.002$		
	Mixed (Combined)	SSR (+) $p < 0.001$		
		SRS (+) $p < 0.001$		
		SLR (+) $p < 0.001$		
		LRS (+) $p < 0.001$		

		SCR (+) p = 0.04 CRS (+) p <0.001	

When binned into the different age classes (1, 2, and 3+), 63 models were compared. Of the 1476 observations, 1086 Lingcod were measured, resulting in 703 year 1, 234 year 2, and 149 year 3+ observations. These 1086 observations were used in subsequent size specific model comparisons to investigate if there is a change in habitat associations with a change in Lingcod size.

When compared using AIC, four models were within two ΔAIC of the top model. However, when the number of parameters was taken into account, there were substantially more in the subsequent models (up to seven parameters) than in the top model (three parameters) indicating that the number of parameters may influence the model ranking. Also, when compared using a Chi-Square, the additional parameters were correlated with one another (e.g. secondary substrate and combined substrate), therefore only the top model was considered ($p > 0.001$).

Year 1 Lingcod had a significant negative association with continuous rock substrate and the combination of low-wave relief, and depth. There was also a significant positive relationship with homogeneous sand and small rock substrates, combinations of sand and small rock with large rock, homogeneous low and wave reliefs. This indicates that lower relief areas and the substrates generally associated with low relief, as well as shallower depths are best for small Lingcod (Table 3). Other variables that were not significant in this model included high and moderate reliefs and most hard substrate types.

Table 3 Significant variables in the best model for year 1 Lingcod. This model included combined substrate, combined relief, and depth. Substrate combinations include: soft (S), small rock (SR), large rock (LR), and continuous rock (CR). Combined relief includes low (L), and wave (W).

	Predictor Variables				
Age Class	Substrate		Relief		Depth
Year 1	Soft (Combined)	SS (+) $p < 0.001$	Combined	LL (+) $p < 0.001$ WW (+) $p < 0.001$ LW (-) $p = 0.029$	(-) $p < 0.001$
	Hard (Combined)	SRSR (+) $p < 0.001$ SRLR (+) $p < 0.001$ CRSR (+) $p = 0.011$ CRCR (-) $p < 0.001$			
	Mixed (Combined)	SSR (+) $p < 0.001$ SRS (+) $p = 0.006$ LRS (+) $p < 0.028$			

Year 2 Lingcod had two models within two ΔAIC of each other. Both models included the variables primary and secondary substrate and combined relief. One model also included depth, but it was not significant.

Both models indicated year 2 Lingcod had a significant negative association with soft substrate and low relief areas (Table 4). Year 2 Lingcod had significant positive associations with the primary and secondary substrates small rock and large rock as well as wave relief, indicating they are associating with areas of increased complexity.

Table 4 Significant variables in the two best models for year 2 Lingcod. Primary and Secondary substrate as well as primary relief are included. Substrate combinations include: soft (S), small rock (SR), and large rock (LR). Wave (W) was the only significant relief type. (*) denotes the variable was only significant in one of the models.

	Predictor Variables				
Age Class	Substrate			Relief	
Year 2	Primary	Soft	S (-) p ≤0.001	Primary	W (+) p = 0.002 L (-) p ≤ 0.001
		Hard	SR (+) * p = 0.003 LR (+) p = 0.002		
	Secondary	Soft	S (-) p ≤0.001		
		Hard	SR (+) * p = 0.029 LR (+) p = 0.002		

A total of five models were within two ΔAIC for year 3+ Lingcod. All models contained primary relief, four contained secondary substrate, three included primary and combined substrate, and one included depth. Two models were removed from consideration after a Chi-square analysis showed correlation between primary and/or secondary substrate with combined substrate ($p > 0.001$).

The remaining three models showed significant negative associations soft sediment and low relief areas (Table 5). Year 3+ Lingcod had a significant positive association with hard and mixed substrates, as well as primary moderate relief. Relief did not have any other significant associations indicating that substrate type may play a more important role in year 3+ Lingcod distribution.

Table 5 Significant variables in the top three models. Predictor variables included primary, secondary, and combined substrate and primary relief. Substrate types include soft (S), small rock (SR), large rock (LR), and continuous rock (CR), both singularly and combined. Relief types include low (L) and moderate (M). (*), (**), and (***) denote presence in one, two, and three of the models respectively.

	Predictor Variables				
Age Class	Substrate			Relief	
Year 3+	Primary	Soft	S (-) ** p <0.001	Primary	L (-) *** p <0.001
		Hard	LR (+) ** p <0.002		M (+) *** p <0.001
	Secondary	Soft	S (-) ** p <0.001		
		Hard	SR (+) ** p <0.001		
			LR (+) ** p <0.001		
			CR (+) ** p ≤0.02		
	Combined	Soft	SS (-) * p <0.001		
		Hard	SRSR (+) * p <0.001		
			SRLR (+) * p = 0.001		
			CRCR (+) * p <0.001		
			CRSR (+) * p = 0.011		
			CRLR (+) * p = 0.003		
			LRSR (+) * p <0.001		
			LRCR (+) * p = 0.009		
			LRLR (+) *		

			$p < 0.001$		
		Mixed	SCR (+) * $p = 0.001$ SLR (+) * $p < 0.001$ SRS (+) * $p = 0.002$		

LANDSCAPE MODELING & HABITAT SUITABILITY MAPPING

A total of 1035 individual Lingcod observations were used in the habitat suitability analysis. The smallest Lingcod in this analysis was 5 cm and the largest was 80 cm long. Depth ranged from19 m to 358 m. A total of 427 year 1, 154 year 2, and 107 year 3+ Lingcod were used to determine if the ontogenetic shift in habitat utilization could be detected in a GIS based analysis. Some individuals observed with the ROV were not sized and therefore were left out of subsequent age class models (n = 347). No observations made with the towed camera sled were used for the habitat suitability modeling because accurate GPS tracking data are necessary to ensure accurate model results. A total of 83 models were run for all size classes of Lingcod.

Three models were within two ΔAIC for all Lingcod (Table 6). All models included the variables distance from rock and depth. Two models included VRM and one model included slope but none were significant ($p > 0.05$). The variables slope and VRM were correlated and not considered in further analyses because their interaction was unknown. The remaining two models showed a significant negative association with distance from rock ($p < 0.001$) and significant positive association with depth ($p < 0.001$) (Figure 2).

Table 6 AIC table for the top three all Lingcod models including variable coefficients. All three models contained distance from rock and depth. Both of these variables were also significant in the models. Models 41 and 60 also contained VRM and VRM and slope respectively, but neither variable was significant.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
M41				4	2724.76	2724.78	0	0.346
	VRM	-0.117	0.09					
	Distance from rock	-0.385	> 0.001					
	Depth	0.002	> 0.001					
M21				3	2725.86	2725.87	1.08	0.212
	Distance from rock	-3.00×10^{-4}	> 0.001					
	Depth		> 0.001					
M60				5	2726.65	2726.68	1.89	0.141
	VRM	-0.145	0.119					
	Distance from rock	-3.13×10^{-4}	> 0.001					
	Depth	0.002	> 0.001					
	Slope	0.003	0.739					

Two models for year 1 Lingcod were within two ΔAIC (Table 7). Both showed a significant negative association with slope ($p < 0.001$) and TPI_{40} ($p < 0.001$) (Figure 2B). One model also included north as a predictor variable, but it was not significant ($p = 0.25$).

Table 7 AIC table for the top two year 1 Lingcod models including variable coefficients. Both models contained slope and TPI40 as significant variables. Model 49 also contained the variable north, but it was not significant.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
Y1M25				3	1129.43	1129.44	0.00	0.255
	Slope	-0.088	> 0.001					
	TPI_{40}	-0.731	> 0.001					
Y1M49				4	1130.11	1130.13	0.69	0.118
	Slope	-0.084	> 0.001					
	North	0.127	0.25					
	TPI_{40}	-0.737	> 0.001					

Nine models were within the two ΔAIC for year 2 Lingcod (Table 8). All models showed significant negative associations with distance from rock, indicating that year 2 Lingcod had a positive association with areas close to hard substrate ($p \leq 0.001$) (Figure 2C). Other models included the predictor variables VRM, north, east, TPI_{20}, TPI_{40}, and slope, but none were significant ($p > 0.05$).

Table 8 AIC table for the top nine year 2 Lingcod models including variable coefficients. The consistent and only significant variable in all models was distance from rock.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
Y2M2				2	389.30	389.30	0.00	0.107
	Distance from rock	-0.002	> 0.001					
Y2M18				3	389.81	389.82	0.52	0.082
	Distance from rock	-0.002	> 0.001					
	East	0.211	0.223					
Y2M20				3	390.01	390.02	0.72	0.074
	Distance from rock	-0.002	> 0.001					
	TPI_{40}	0.274	0.267					
Y2M16				3	390.11	390.12	0.81	0.071
	Distance from rock	-0.002	> 0.001					
	Slope	0.028	0.286					
Y2M17				3	390.70	390.72	1.41	0.052
	Distance from rock	-0.002	> 0.001					
	North	-0.137	0.441					
Y2M43				4	391.01	391.03	1.73	0.045
	Distance from rock	-0.002	> 0.001					
	Slope	0.023	0.38					
	East	0.184	0.295					
Y2M19				3	391.21	391.22	1.92	0.04
	Distance from rock	-0.002	> 0.001					
	TPI_{20}	0.096	0.765					
Y2M9				3	391.27	391.28	1.98	0.039
	Distance from rock	-0.002	> 0.001					
	VRM	6.858	0.873					
Y2M21				3	391.28	391.30	1.99	0.039
	Distance from rock	-0.002	> 0.001					
	Depth	2×10^{-4}	0.907					

Year 3+ Lingcod had two models within two ΔAIC (Table 9). Both models included distance from rock, slope, and depth and one included VRM. Year 3+ Lingcod had a significant positive association with distance from rock ($p \leq 0.05$), slope ($p < 0.001$), and depth ($p \leq 0.05$), while they had a significant negative association with VRM ($p = 0.43$). These results imply that year 3+ Lingcod have a positive association with steep, deep areas that are close to hard substrate (Figure 2D).

Table 9 AIC table for the top two year 3+ Lingcod models including variable coefficients. Models 46 and 60 both contained the variables: distance from rock, slope and depth. Model 60 also contained VRM, but it was not significant.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
Y3M46				4	259.49	259.51	0.00	0.288
	Distance from rock	-0.001	0.027					
	Slope	0.173	> 0.001					
	Depth	0.008	0.025					
Y3M60				5	260.72	260.75	1.24	0.155
	Distance from rock	-0.001	0.027					
	Slope	0.159	0.001					
	Depth	0.007	0.029					
	VRM	62.246	0.436					

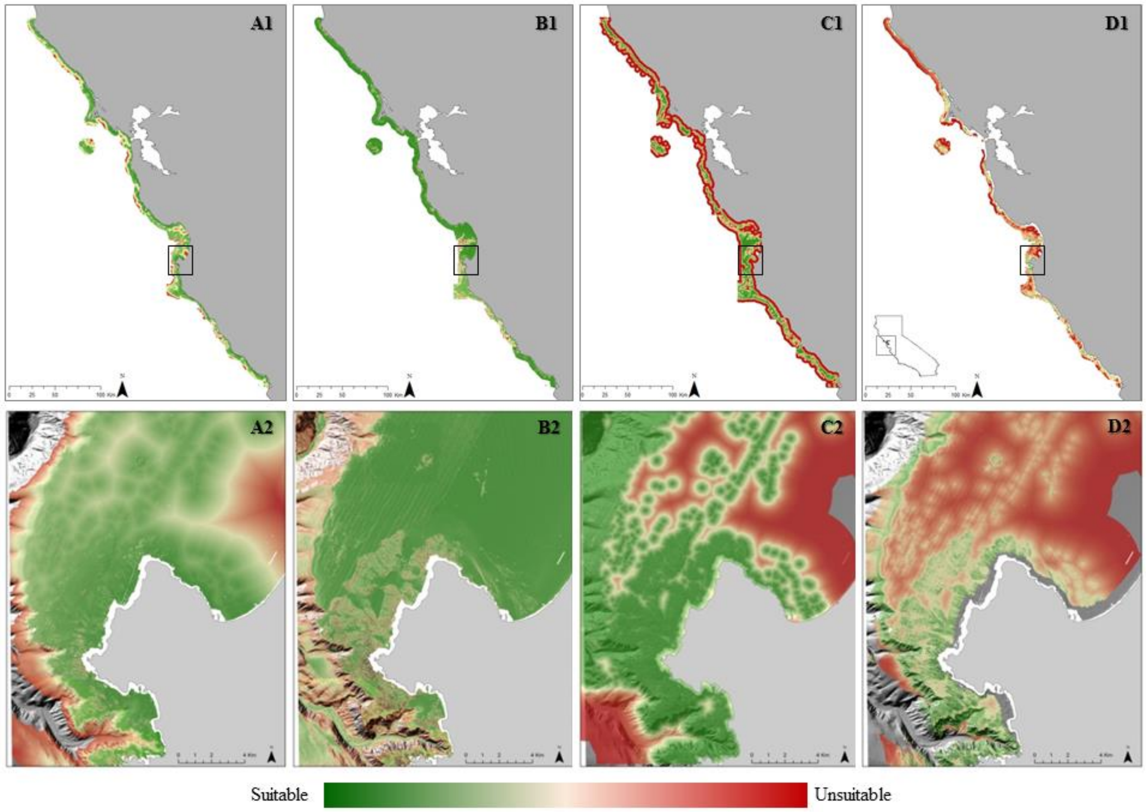

Figure 2 Habitat suitability models for A1) all Lingcod; B1) year 1 Lingcod; C1) year 2 Lingcod; and D1) year 3+ Lingcod over the entire study area. A2) all Lingcod; B2) year 1 Lingcod; C2) year 2 Lingcod; and D2) year 3+ show a zoomed-in view of the Monterey Peninsula. The all Lingcod maps show that there are a wide variety of suitable (green) habitat types, with more suitable habitat surrounding hard substrate. Suitable habitat for year 1 Lingcod is predominately in the soft substrate areas. Rocky reefs are red, indicating highly unsuitable habitat. Year 2 Lingcod suitable habitat is concentrated on and around hard substrate. Year 3+ Lingcod have a similar pattern as year 2, with less of a halo around hard substrate, indicating that soft sediment is unsuitable habitat.

CHAPTER 4

DISCUSSION AND CONCLUSIONS

DISCUSSION

The results of this study clearly depicted an ontogenetic shift in Lingcod habitat utilization across the southern portion of its range. Lingcod shifted from primarily low relief, soft sediments as young to mixed substrates at intermediate ages and ultimately to primarily harder substrates as adults. Direct video observations confirmed these patterns while observations coupled to high-resolution topographic maps depicted how Lingcod are likely to use the habitats beyond sampled transects. These results are important in the context of on-going marine spatial planning efforts wherein more refined spatial data can allow for more refined management, for example re-defining spatial closures. However, the size-age ratios used for this study were from a study conducted by Shaw and Hassler in Washington and Oregon (1989). This study did not seek to validate the age-length ratios previously published; we suggest a study focused on Lingcod growth rates in California be conducted to validate age-length ratios used to determine the ontogenetic shift found in this study.

Small, year 1 Lingcod were positively associated with shallow, homogenous soft sediment and low and wave relief areas. This aligns with the current understanding of small Lingcod, as Petrie and Ryer (2006) found that post-settlement Lingcod were predominately found in sandy areas adjacent to eelgrass beds in Yaquina Bay, Oregon. However, year 1 Lingcod were also positively associated with homogenous small rock and mixed substrate types. Small Lingcod associating with these hard substrate types has not been documented before to our knowledge. This association may be due to a lack of eelgrass beds, which serve as structure for small Lingcod, or a factor of this study exploring habitats outside of eelgrass beds. Many studies state that small, year 1 Lingcod, live in the shallows near vegetation such as kelp or eelgrass beds (Phillips and Barraclough 1977; Cass et al. 1990). However, eelgrass beds are highly susceptible to anthropogenic impacts, resulting in loss of this already sparse ecosystem (Williams and Davis 2006). With the lack of eelgrass beds in California, small Lingcod may select other structurally complex habitats such as the hard and mixed substrate types found in this study. This study did investigate the outer kelp forest habitats, but did not explore any eelgrass beds. Finding small Lingcod associating with habitat types outside of what is discussed in the literature may be a factor of looking in different areas than previous studies, thus expanding our knowledge of Lingcod habitat associations.

All but one other study on Lingcod have been conducted from Oregon to Alaska (Mathews and LaRiviere 1987; Cass et al. 1990; Jagielo 1990; Matthews 1992; O'Connell 1993; Yamanaka and Richards 1993; Martell et al. 2000; Pacunski and Palsson 2001; Starr et al. 2005; Petrie and Ryer 2006; Beaudreau and Essington 2007; Tolimieri et al. 2009) therefore, it is important to think critically about the assumptions we make for Lingcod populations in California. There are differences in the oceanographic conditions and habitat availability along Lingcod's range that should be considered when extrapolating current knowledge on the habitat associations of Lingcod.

Year 2 Lingcod had negative associations with soft substrate and low relief areas, contrary to year 1 Lingcod. Year 2 Lingcod had a positive association with large and small rock substrates as well as the heterogeneous combinations of moderate and low relief. This is in agreement with Cass et al.'s (1990) findings in the Strait of Georgia, where they documented year 2 Lingcod resided in similar habitats as larger Lingcod, but may stay in shallower depths to avoid predation by larger individuals.

The significant positive association of year 2 Lingcod with homogenous wave relief has not been documented in previous studies. Year 2 Lingcod may not associate with the wave relief as a habitat measure, but rather as a source of prey. Beaudreau and Essington (2007) found rockfish consistently in the stomach contents of Lingcod larger than 30 cm. Hallenbeck et al. (2012) found large numbers of small Canary Rockfish in features called rippled-scour depressions in Monterey Bay, California. The juvenile fishes that reside in these coarse-grain soft sediment areas could be attracting year 2 Lingcod.

Although year 3+ Lingcod had a positive association with hard substrate, they did not demonstrate the same association with depth as Starr et al.'s (2005) paper documented in Alaska. Starr et al. (2005) found large, reproductive Lingcod generally inhabited deeper waters, and females mainly came in shallower depths to lay their eggs. Our study did not seek to investigate potential habitat shifts made by different sexes or seasonally. We did not attempt to sex individuals observed on video, as it requires observing the presence (male) or absence (female) of small external papillae. We also did not investigate any potential seasonal changes in habitat use. No video was collected during the Lingcod mating and nest-guarding season (November through March) (King and Withler 2005), therefore we assumed no change in habitat utilization for non-reproducing Lingcod.

The GIS model results paralleled those of the visual analysis. As many of the predictor variables are similar, this result was expected. VRM, slope, and TPI could be considered aspects of relief and distance from rock is a proxy for hard and soft substrate. As with the visual analysis, all Lingcod in the GIS analysis associated with shallow, complex areas close to hard substrate. This finding highlights the necessity to investigate size-specific habitat associations, as it completely neglects the habitat associations of year 1 Lingcod. It is important to understand these more nuanced relationships with various habitat types, especially when protecting a species through spatial management strategies, as in the case of Lingcod.

Although the two techniques resulted in similar findings, it is important to note the video analysis was at a much finer scale (sub meter), while the GIS analysis was at a 5 meter scale. As such, the video analysis allowed us to put context to the larger scale GIS analysis. For example, the GIS analysis for year 1 Lingcod showed a significant negative association with slope and TPI, while the video analysis showed a positive association with soft and mixed sediments, as well as low and wave relief types. The finer scale analysis allows us to get more in-depth information on specific habitat associations and the GIS analysis allows for a visual representation of the models in a map form. We suggest, when possible, for a combination of both techniques to get a complete understanding of habitat associations of a particular species.

Currently, Lingcod are managed spatially through the establishment of rockfish conservation areas (RCAs), which provide refuge for many groundfish species from fishing pressure as mandated by Pacific Fisheries Management Council. However, if these spatial closures are only protecting a portion of the life history of Lingcod, their populations may still be vulnerable without other fisheries management measures (e.g. size limits). When creating spatial management plans for any species, it is critical to understand what drives their distribution as much as possible and how those drivers may differ over a large geographic range. As more information about habitat distribution and the species that associate with those habitats becomes available, it is important to re-evaluate current management boundaries with updated knowledge. Many spatial management strategies incorporate adaptive management, allowing for re-evaluation as more information becomes available.

Many Lingcod studies have been conducted using acoustic tagging and focused on smaller areas than in this study, e.g.: a particular acoustic array (Starr et al. 2005; Tolimieri et al. 2009). This study spanned a large geographic and depth range, therefore alleviating any possible associations specific to a small population of Lingcod, and strengthened our extrapolations into areas beyond our transects. It is important to couple different techniques to understand the entirety of a species life history and habitat requirements. Acoustic tagging has allowed us to understand the movement patterns of Lingcod over a variety of scales both temporal and spatial (Jagielo 1990; Lee et al. 2011; Andrews et al. 2011). Coupling our knowledge gained from acoustic tagging with the knowledge gained from visual observations in this study allow us to better understand what habitats Lingcod are utilizing.

CONCLUSION

This study provides insight on the specific habitat associations of Lingcod at various life stages, as well as spatially explicit models of these findings for a geographic area where little work has been conducted. We validated the current understanding of Lingcod habitat associations, but highlighted that these associations may be more nuanced than previously thought. Understanding the differences in habitat associations across a large geographic range is especially important for a spatially managed species. While Lingcod in California had similar habitat associations as individuals further north, this study highlighted that subtle shifts in habitat availability may alter how one life stage associates with the environment. These differences in associations over a large geographic range must be taken into account to insure informed spatial management plans.

This study also highlighted the utility of combining multiple methods when investigating habitat associations. The visual analysis resulted in fine-scale habitat associations (e.g. specific types of hard substrate), while the landscape modeling analysis allowed for extrapolation to areas not surveyed in this study. The GIS analysis and subsequent suitability maps also allow for spatial analyses around current and proposed management boundaries. The utility of suitability maps is made apparent when working with other stakeholders, such as the public or resource management agencies and coupling them with fine-scale habitat associations creates a more holistic view of a species' habitat needs.

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APPENDIX A

SUPPLIMENTAL AIC TABLES

Table 10 AIC table for the visual analysis of all Lingcod. One model was within two ΔAIC of the other models.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
M66				23	1576.043	1576.416	0	7.52E-01
	Prel- H	2.68	0.001					
	Prel- M	0.54	0.008					
	Prel- W	0.48	0.258					
	Prel- L	-2.69	> 0.001					
	Srel- H	4.12	> 0.001					
	Srel- M	0.51	0.011					
	Srel- W	1.08	> 0.001					
	Srel- L	-2.69	> 0.001					
	Csub-CRCR	0.70	0.002					
	Csub- CRLR	1.49	0.003					
	Csub- CRS	1.54	> 0.001					
	Csub-CRSR	1.72	> 0.001					
	Csub- LRCR	2.26	> 0.001					
	Csub- LRLR	2.63	> 0.001					
	Csub- LRS	2.86	> 0.001					
	Csub- LRSR	2.35	> 0.001					
	Csub- SCR	1.07	0.040					
	Csub- SLR	1.89	> 0.001					
	Csub- SRCR	-20.62	0.999					
	Csub-SRLR	3.38	> 0.001					
	Csub- SRS	2.64	> 0.001					
	Csub- SRSR	1.59	> 0.001					
	Csub- SSR	1.78	> 0.001					
	Csub- SS	-2.69	> 0.001					

Table 11 AIC table for the visual analysis of year 1 Lingcod. A total of five models were within two ΔAIC of the other models.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
Y1.M43				29	1689.826	1691.061	0	2.00E-01
	Csub- SS	0.79	> 0.001					
	Csub-	-1.83	> 0.001					

	CRCR							
	Csub-CRLR	0.03	0.959					
	Csub- CRS	-0.01	0.987					
	Csub-CRSR	-2.50	0.019					
	Csub-LRCR	-0.14	0.825					
	Csub-LRLR	1.17	0.002					
	Csub- LRS	1.15	0.049					
	Csub-LRSR	0.77	0.048					
	Csub- SCR	-0.35	0.380					
	Csub- SLR	0.22	0.596					
	Csub-SRCR	-1.60	0.158					
	Csub-SRLR	2.01	0.002					
	Csub- SRS	0.52	0.138					
	Csub-SRSR	1.16	> 0.001					
	Csub- SSR	0.78	0.001					
	Crel-HH	13.72	0.988					
	Crel-HL	13.35	0.983					
	Crel-HM	-13.02	0.988					
	Crel-LH	16.37	0.985					
	Crel-LM	-0.69	0.049					
	Crel-LW	-0.80	0.004					
	Crel-MH	1.65	0.227					
	Crel-ML	0.50	0.162					
	Crel-MM	0.13	0.767					
	Crel-WL	-0.96	0.281					
	Crel-WM	-14.64	0.987					
	Crel-WW	1.60	> 0.001					
	Crel-LL	0.79	> 0.001					
	Depth	0.01	> 0.001					
Y1.M53				29	1689.826	1691.061	0	2.00E-01
	Prel-H	-5.4×10^{12}	0.943					
	Prel-M	-5.4×10^{12}	0.943					
	Prel-W	-0.96	0.281					
	Prel-L	0.79	> 0.001					
	Srel-H	5.4×10^{12}	0.943					
	Srel-M	5.4×10^{12}	0.943					
	Srel-W	2.56	0.007					
	Srel-L	0.79	> 0.001					
	Csub-CRCR	-1.83	> 0.001					
	Csub-CRLR	0.03	0.960					
	Csub-CRSR	0.00	0.989					
	Csub-CRSR	-2.50	0.020					
	Csub-LRCR	-0.14	0.824					
	Csub-LRLR	1.16	0.002					
	Csub-LRS	1.15	0.049					
	Csub-LRSR	0.77	0.048					
	Csub-CSR	-0.35	0.380					

	Csub-SLR	0.22	0.596					
	Csub-SRSR	-1.60	0.157					
	Csub-SRLR	2.01	0.002					
	Csub-SRS	0.52	0.138					
	Csub-SRSR	1.16	> 0.001					
	Csub-SSR	0.78	0.001					
	Csub-SS	0.79	> 0.001					
	Crel-HH	4.5×10^{15}	> 0.001					
	Crel-HL	5.4×10^{12}	0.943					
	Crel-LH	-5.4×10^{12}	0.943					
	Crel-LM	-5.4×10^{12}	0.943					
	Crel-LW	-3.36	0.001					
	Crel-ML	5.4×10^{12}	0.943					
	Crel-WM	-5.4×10^{12}	0.943					
	Crel-LL	0.79	> 0.001					
	Depth	0.01	> 0.001					
Y1.M59				29	1689.826	1691.061	0	2.00E-01
	Prel-H	-5.4×10^{12}	0.943					
	Prel-M	-5.4×10^{12}	0.943					
	Prel-W	-0.956	0.281					
	Prel-L	0.793	> 0.001					
	Srel-H	5.4×10^{12}	0.943					
	Srel-M	5.4×10^{12}	0.943					
	Srel-W	2.559	0.007					
	Srel-L	0.793	> 0.001					
	Csub-CRCR	-1.830	> 0.001					
	Csub-CRLR	0.028	0.960					
	Csub-CRSR	-0.005	0.989					
	Csub-CRSR	-2.496	0.020					
	Csub-LRCR	-0.137	0.824					
	Csub-LRLR	1.163	0.002					
	Csub-LRS	1.150	0.049					
	Csub-LRSR	0.774	0.048					
	Csub-CSR	-0.352	0.380					
	Csub-SLR	0.220	0.596					
	Csub-SRSR	-1.601	0.157					
	Csub-SRLR	2.007	0.002					
	Csub-SRS	0.522	0.138					
	Csub-SRSR	1.160	0.000					
	Csub-SSR	0.777	0.001					
	Csub-SS	0.793	> 0.001					
	Crel-HH	4.5×10^{15}	> 0.001					
	Crel-HL	5.4×10^{12}	0.943					
	Crel-LH	-5.4×10^{12}	0.943					
	Crel-LM	-5.4×10^{12}	0.943					
	Crel-LW	-3.355	0.001					
	Crel-ML	5.4×10^{12}	0.943					
	Crel-WM	-5.4×10^{12}	0.943					

	Crel-LL	0.793	> 0.001					
	Depth	0.012	> 0.001					
Y1.M62				29	1689.826	1691.061	0	2.00E-01
		0.793	> 0.001					
	Ssub-CR	-1.601	0.158					
	Ssub-LR	2.007	0.002					
	Ssub-SR	0.777	0.001					
	Ssub-S	0.793	> 0.001					
	Prel-H	0.660	1.000					
	Prel-M	13.810	0.988					
	Prel-W	-0.955	0.281					
	Prel-L	0.793	> 0.001					
	Srel-H	-12.170	0.989					
	Srel-M	-13.680	0.988					
	Srel-W	2.559	0.007					
	Srel-L	0.793	> 0.001					
	Csub-CRCR	-0.229	0.842					
	Csub-CRLR	-1.978	0.017					
	Csub-CRS	-0.006	0.987					
	Csub-CRSR	-3.273	0.003					
	Csub-LRCR	1.465	0.251					
	Csub-LRLR	-0.840	0.235					
	Csub-LRS	1.149	0.049					
	Csub-LRSR	-0.002	0.996					
	Csub-SCR	1.248	0.295					
	Csub-SLR	-1.787	0.019					
	Csub-SRS	0.522	0.138					
	Csub-SRSR	0.384	0.251					
	Csub-SS	0.793	> 0.001					
	Crel-HH	25.230	0.984					
	Crel-HL	12.690	0.993					
	Crel-LH	28.530	0.982					
	Crel-LM	12.990	0.988					
	Crel-LW	-3.355	0.001					
	Crel-ML	-13.310	0.988					
	Crel-LL	0.793	> 0.001					
	Depth	0.012	> 0.001					
Y1.M63				29	1689.826	1691.061	0	2.00E-01
	Psub-CR	-3.273	0.003					
	Psub-LR	-0.002	0.996					
	Psub-SR	0.384	0.251					
	Psub-S	0.793	>0.001					
	Ssub-CR	-1.984	0.093					
	Ssub-LR	1.623	0.026					
	Ssub-SR	0.777	0.001					
	Ssub-S	0.793	>0.001					
	Prel-H	0.660	1.000					
	Prel-M	13.810	0.988					
	Prel-W	-0.955	0.281					
	Prel-L	0.793	>0.001					
	Prel-H	-12.170	0.989					
	Prel-M	-13.680	0.988					

Prel-W	2.559	0.007
Prel-L	0.793	>0.001
Csub-CRCR	3.428	0.030
Csub-CRLR	1.679	0.219
Csub-CRS	3.267	0.004
Csub-LRCR	1.851	0.170
Csub-LRLR	-0.454	0.584
Csub-LRS	1.150	0.105
Csub-SCR	1.632	0.188
Csub-SLR	-1.403	0.090
Csub-SRS	0.138	0.775
Csub-SS	0.793	>0.001
Crel-HH	25.230	0.984
Crel-HL	12.690	0.993
Crel-LH	28.530	0.982
Crel-LM	12.990	0.988
Crel-LW	-3.355	0.001
Crel-ML	-13.310	0.988
Crel-LL	0.793	>0.001
Depth	0.012	> 0.001

Table 12 AIC table for the visual analysis of year 2 Lingcod. A total of 3 models were within two ΔAIC of the other models.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
Y2.M32				15	548.6377	549.6903	0	2.48E-01
	Psub-CR	0.400	0.318					
	Psub-LR	1.481	> 0.001					
	Psub-SR	0.532	0.163					
	Psub-SR	-1.008	> 0.001					
	Ssub-CR	-0.052	0.896					
	Ssub-LR	1.665	> 0.001					
	Ssub-SR	0.951	0.006					
	Ssub-S	-1.008	> 0.001					
	Crel-HH	16.227	0.982					
	Crel-HL	14.142	0.992					
	Crel-LM	0.659	0.150					
	Crel-LW	-0.685	0.402					
	Crel-ML	1.248	0.006					
	Crel-MM	0.492	0.410					
	Crel-WL	-15.286	0.984					
	Crel-WW	2.197	> 0.001					
	Crel-LL	-1.008	> 0.001					

Y2.M46				15	548.6377	549.6903	0	2.48E-01
	Psub-CR	0.400	0.318					
	Psub-LR	1.481	> 0.001					
	Psub-SR	0.532	0.163					
	Psub-S	-1.008	> 0.001					
	Ssub-CR	-0.052	0.896					
	Ssub-LR	1.665	> 0.001					
	Ssub-SR	0.951	0.006					
	Ssub-S	-1.008	> 0.001					
	Prel-H	14.142	0.992					
	Prel-M	0.492	0.410					
	Prel-W	2.197	> 0.001					
	Prel-L	-1.008	> 0.001					
	Crel-HH	2.084	0.999					
	Crel-LM	0.659	0.150					
	Crel-LW	-0.685	0.402					
	Crel-ML	0.756	0.271					
	Crel-WL	-17.484	0.982					
	Crel-LL	-1.008	> 0.001					
Y2.M55				15	548.6377	549.6903	0	2.48E-01
	Psub-CR	0.400	0.318					
	Psub-LR	1.481	> 0.001					
	Psub-SR	0.532	0.163					
	Psub-S	-1.008	> 0.001					
	Ssub-CR	-0.052	0.896					
	Ssub-LR	1.665	> 0.001					
	Ssub-SR	0.951	0.006					
	Ssub-S	-1.008	> 0.00					
	Prel-H	14.142	0.992					
	Prel-M	1.248	0.006					
	Prel-W	-15.286	0.984					
	Prel-L	-1.008	> 0.001					
	Prel-H	2.084	0.999					
	Prel-M	-0.756	0.271					
	Prel-W	17.484	0.982					
	Prel-L	-1.008	> 0.001					
	Crel-LM	1.414	0.080					
	Crel-LW	-18.169	0.981					
	Crel-LL							

Table 13 AIC table for the visual analysis of year 3+ Lingcod. Only one model was within two ΔAIC of the other models.

Model	Variable	Coefficient	p-value	df	AIC	AICc	ΔAIC	AICw
Y3.M20				19	307.7284	310.4427	0.00E+00	2.10E-01
	Prel-H	17.521	0.990					
	Prel-M	0.846	0.058					
	Prel-W	1.173	0.171					
	Prel-L	-1.966	> 0.001					
	Csub-CRCR	1.478	> 0.001					
	Csub-CRLR	2.012	0.008					
	Csub-CRS	0.779	0.400					
	Csub-CRSR	2.896	0.016					
	Csub-LRCR	19.150	0.992					
	Csub-LRLR	3.500	> 0.001					
	Csub-LRS	2.797	0.002					
	Csub-LRSR	4.249	> 0.001					
	Csub-SCR	1.629	0.015					
	Csub-SLR	2.524	0.001					
	Csub-SRLR	19.532	0.991					
	Csub-SRS	2.659	0.004					
	Csub-SRSR	3.912	> 0.001					
	Csub-SSR	2.920	> 0.001					
	Csub-SS	-1.966	> 0.001					

APPENDIX B

EXAMPLE R CODE FOR GLM MODELING & AIC ANALYSIS

```
# Import Data
ling <- read.csv(file.choose(), header = T)

# Fill in NAs with 0
ling[is.na(ling)]<- 0
```

```r
# Create AIC comparison table
AICtable <- function( aic, n) {
K <- aic$df
AICc <- aic$AIC + 2 * K * (K+1) / ( n - K - 1 )
delAIC<- AICc - min( AICc )
AICw <- exp(-0.5*delAIC) / sum( exp(-0.5*delAIC))
data.frame( aic, AICc, delAIC , AICw)
}
# Re-level categories. Make soft sediment and low relief the intercept
ling$Psubl <- relevel(ling$Psub, ref = "s")
ling$Ssubl <- relevel(ling$Ssub, ref = "s")
ling$Prell <- relevel(ling$Prel, ref = "l")
ling$Srell <- relevel(ling$Srel, ref = "l")
ling$Csubl <- relevel(ling$Csub, ref = "ss")
ling$Crell <- relevel(ling$Crel, ref = "ll")

# Run GLMs for all sizes
M0  <- glm(ling$Count ~ 1, family=binomial)
M1  <- glm(ling$Count ~ ling$Psubl, family=binomial)
M2  <- glm(ling$Count ~ ling$Ssubl, family=binomial)
M3  <- glm(ling$Count ~ ling$Prell, family=binomial)
M4  <- glm(ling$Count ~ ling$Srell, family=binomial)
M5  <- glm(ling$Count ~ ling$Csubl, family=binomial)
M6  <- glm(ling$Count ~ ling$Crell, family=binomial)
M7  <- glm(ling$Count ~ ling$Depth, family=binomial)
M8  <- glm(ling$Count ~ ling$Size,  family=binomial)
M9  <- glm(ling$Count ~ ling$Psubl + ling$Ssubl, family=binomial)
M10 <- glm(ling$Count ~ ling$Psubl + ling$Prell, family=binomial)
M11 <- glm(ling$Count ~ ling$Psubl + ling$Srell, family=binomial)
M12 <- glm(ling$Count ~ ling$Psubl + ling$Csubl, family=binomial)
M13 <- glm(ling$Count ~ ling$Psubl + ling$Crell, family=binomial)
M14 <- glm(ling$Count ~ ling$Psubl + ling$Depth, family=binomial)
M15 <- glm(ling$Count ~ ling$Psubl + ling$Size,  family=binomial)
M16 <- glm(ling$Count ~ ling$Ssubl + ling$Prell, family=binomial)
M17 <- glm(ling$Count ~ ling$Ssubl + ling$Srell, family=binomial)
M18 <- glm(ling$Count ~ ling$Ssubl + ling$Csubl, family=binomial)
M19 <- glm(ling$Count ~ ling$Ssubl + ling$Crell, family=binomial)
```

```
M20 <- glm(ling$Count ~ ling$Ssubl + ling$Depth, family=binomial)
M21 <- glm(ling$Count ~ ling$Ssubl + ling$Size,  family=binomial)
M22 <- glm(ling$Count ~ ling$Prell + ling$Srell, family=binomial)
M23 <- glm(ling$Count ~ ling$Prell + ling$Csubl, family=binomial)
M24 <- glm(ling$Count ~ ling$Prell + ling$Crell, family=binomial)
M25 <- glm(ling$Count ~ ling$Prell + ling$Depth, family=binomial)
M26 <- glm(ling$Count ~ ling$Prell + ling$Size,  family=binomial)
M27 <- glm(ling$Count ~ ling$Srell + ling$Csubl, family=binomial)
M28 <- glm(ling$Count ~ ling$Srell + ling$Crell, family=binomial)
M29 <- glm(ling$Count ~ ling$Srell + ling$Depth, family=binomial)
M30 <- glm(ling$Count ~ ling$Srell + ling$Size,  family=binomial)
M31 <- glm(ling$Count ~ ling$Csubl + ling$Crell, family=binomial)
M32 <- glm(ling$Count ~ ling$Csubl + ling$Depth, family=binomial)
M33 <- glm(ling$Count ~ ling$Csubl + ling$Size,  family=binomial)
M34 <- glm(ling$Count ~ ling$Crell + ling$Depth, family=binomial)
M35 <- glm(ling$Count ~ ling$Crell + ling$Size,  family=binomial)
M36 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell,
      family=binomial)
M37 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Srell,
      family=binomial)
M38 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl +ling$Csubl,
      family=binomial)
M39 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl +ling$Crell,
      family=binomial)
M40 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Depth,
      family=binomial)
M41 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Size,
      family=binomial)
M42 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell,
      family=binomial)
M43 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Csubl,
      family=binomial)
M44 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Crell,
      family=binomial)
M45 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Depth,
      family=binomial)
M46 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Size,
```

```
      family=binomial)
M47 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl,
      family=binomial)
M48 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Crell,
      family=binomial)
M49 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Depth,
      family=binomial)
M50 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Size,
      family=binomial)
M51 <- glm(ling$Count ~ ling$Srell + ling$Csubl + ling$Crell,
      family=binomial)
M52 <- glm(ling$Count ~ ling$Srell + ling$Csubl + ling$Depth,
      family=binomial)
M53 <- glm(ling$Count ~ ling$Srell + ling$Csubl + ling$Size,
      family=binomial)
M54 <- glm(ling$Count ~ ling$Csubl + ling$Crell + ling$Depth
      family=binomial)
M55 <- glm(ling$Count ~ ling$Csubl + ling$Crell + ling$Size,
      family=binomial)
M56 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Srell,
      family=binomial)
M57 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Csubl,
      family=binomial)
M58 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Crell,
      family=binomial)
M59 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell ling$Depth,
      family=binomial)
M60 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Size,
      family=binomial)
M61 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Csubl,
      family=binomial)
M62 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Crell,
      family=binomial)
M63 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Depth,
      family=binomial)
M64 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Crell,
      family=binomial)
```

```
M65 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Depth,
      family=binomial)
M66 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Size,
      family=binomial)
M67 <- glm(ling$Count ~ ling$Srell + ling$Csubl + ling$Crell + ling$Depth,
      family=binomial)
M68 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Srell
      + ling$Csubl, family=binomial)
M69 <- glm(ling$Count ~   ling$Psubl + ling$Ssubl + ling$Prell +
      ling$Srell + ling$Crell, family=binomial)
M70 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Srell
      + ling$Depth, family=binomial)
M71 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Srell
       + ling$Size, family=binomial)
M72 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Csubl
       + ling$Crell, family=binomial)
M73 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Csubl
       + ling$Depth, family=binomial)
M74 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Csubl
       + ling$Size, family=binomial)
M75 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Crell
       + ling$Depth, family=binomial)
M76 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Crell
       + ling$Size, family=binomial)
M77 <- glm(ling$Count ~ ling$Psubl + ling$Ssubl + ling$Prell + ling$Srell
       + ling$Csubl + ling$Crell, family=binomial)
M78 <- glm(ling$Count ~   ling$Psubl + ling$Ssubl + ling$Prell +
       ling$Srell + ling$Csubl + ling$Depth, family=binomial)
M79 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Crell
       + ling$Size, family=binomial)
M80 <- glm(ling$Count ~ ling$Ssubl + ling$Prell + ling$Srell + ling$Csubl
       + ling$Crell + ling$Depth, family=binomial)
M81 <- glm(ling$Count ~ ling$Prell + ling$Srell + ling$Csubl + ling$Crell
       + ling$Size,  family=binomial)
M82 <- glm(ling$Count ~   ling$Psubl + ling$Ssubl + ling$Prell +
      ling$Srell + ling$Csubl + ling$Crell + ling$Depth, family=binomial)
M83 <- glm(ling$Count ~   ling$Psubl + ling$Ssubl + ling$Prell +
```

```
      ling$Srell + ling$Csubl + ling$Crell + ling$Depth + ling$Size,
      family=binomial)
AIC <- AICtable (AIC( M0, M1, M2, M3, M4, M5, M6, M7, M8, M9, M10, M11, M12,
M13, M14, M15, M16, M17, M18, M19, M20, M21, M22, M23, M24, M25, M26, M27,
M28, M29, M30, M31, M32, M33, M34, M35, M36, M37, M38, M39, M40, M41, M42,
M43, M44, M45, M46, M47, M48, M49, M50, M51, M52, M53, M54, M55, M56, M57,
M58, M59, M60, M61, M62, M63, M64, M65, M66, M67, M68, M69, M70, M71, M72,
M73, M74, M75, M76, M77, M78, M79, M80, M81, M82, M83),length(M0$residuals))

#Create a presence and absence tables
ling.abs <- ling[ling$Count < 1,]
ling.pres <- ling[ling$Count > 0,]

# Create Y1 size classes using:
ling.Y1abs <- ling.abs[sample(1:nrow(ling.abs), 735, replace = FALSE),]
# Create the correct number of absence points
ling.Y1pres <- ling[ling$Size<=30 & ling$Size >1,]
# Call out the presence points that are <= 30 cm (735 obs)
# Combine both presence and absence tables into 1 table
ling.Y1 <- rbind(ling.Y1abs, ling.Y1pres)

# Create Y2 size classes using:
ling.Y2abs <- ling.abs[sample(1:nrow(ling.abs), 238, replace = FALSE),]
# Create the correct number of absence points
ling.Y2pres <- ling[ling$Size <= 45 & ling$Size >30,]
#call out the presence points that are >30cm & <= 45cm (238 obs)
# Combine both presence and absence tables into 1 table
ling.Y2 <- rbind(ling.Y2abs, ling.Y2pres)

# Create Y3 size classes using:
ling.Y3abs <- ling.abs[sample(1:nrow(ling.abs), 151, replace = FALSE),]
# Create the correct number of absence points
ling.Y3pres <- ling[ling$Size >45,]
# Combine both presence and absence tables into 1 table
ling.Y3 <- rbind(ling.Y3abs, ling.Y3pres)
```

```
# Use the same models as above to run GLMs for different size classes
(excluding the size variable)
# Use the same code to run GLMs and AIC analyses for landscape modeling using
the variables: ling.gis$vrm5m; ling.gis$dist5m; ling.gis$slope5m;
ling.gis$north5m; ling.gis$east5m; ling.gis$tpi205m; ling.gis$tpi405m;
ling.gis$depth5m)
```